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Life expectancy of wild ruminants in zoological institutions

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Zusammenfassung

In der vorliegenden Studie wurden Daten des "International Species Information Systems" verwendet, um die relative Lebenserwartung (rLE; durchschnittliche Lebenserwartung einer Art als Proportion des Altersrekords) von 78 Wiederkäuerarten in Gefangenschaft zu ermitteln. Dieser Wert reflektiert den jeweiligen Haltungserfolg. Die vergleichende Analyse der rLE verschiedener Arten ermöglichte es, biologische Merkmale zu identifizieren, die einen Einfluss auf die Lebenserwartung haben. So korrelierte der rLE adulter Weibchen positiv mit dem Anteil an Gras in der natürlichen Äsung einer Art (χ^2 = 8.28, p=0.004). Dies bestätigt die Erfahrung aus der Zoohaltung, dass Laubäser im Vergleich zu Gras- und Mischäsern mehr fütterungsbedingte Probleme zeigen. Höhere rLE erreichten adulte Männchen monogamer Arten (χ^2 = 9.92, p=0.007). Dies weist darauf hin, dass Arten, die daran adaptiert sind, ein Harem oder ein Revier zu verteidigen, intrinsischem, physiologischen Stress ausgesetzt sind, selbst wenn sie nicht in Gesellschaft anderer Männchen gehalten werden. Zudem war der rLE beider Geschlechter höher bei Arten, für die ein internationales Zuchtbuch geführt wird (Weibchen: χ^2 = 8.80, p=0.003, Männchen: χ^2 = 5.52, p=0.019). Dieses Ergebnis zeigt, dass sich *ex-situ* Zuchtprogramme auch positiv auf den Haltungserfolg einer Art auswirken. Sollten die Ergebnisse dieser Studie in den Haltungsregimen von Wildwiederkäuern berücksichtigt werden, könnte deren Haltungserfolg weiter verbessert werden.

Life expectancy of wild ruminants in zoological institutions

Summary

Increasing husbandry success is an important aim of zoological institutions, but evaluation procedures are rare. Here, data of the International Species Information System was used to calculate the relative life expectancy (rLE; life expectancy of a species expressed as proportion of the longevity record) of 78 ruminant species in captivity. This parameter reflects the husbandry success for individual species. A comparative analysis of rLE across species tested for biological characteristics that influence life expectancy in captivity. In adult females, rLE correlated positively with the percentage of grass in a species' natural diet (χ^2 = 8.28, p=0.004). This parameter describes the diet a species is adapted to. Thus, our results confirm the general experience of zoos that browsers have more nutrition-related problems than mixed feeders and grazers. Higher rLE was also achieved in adult males of monogamous species (χ^2 = 9.92, p=0.007), suggesting intrinsic physiological stress in males adapted to defend harems even if not kept with competing males. Furthermore, life expectancy was significantly higher in both sexes of species that were managed by an international studbook (females: χ^2 = 8.80, p=0.003, males: χ^2 = 5.52, p=0.019), indicating a positive effect of ex situ conservation efforts. Considering these results in husbandry regimes of wild ruminants, husbandry success in zoos may be further improved.

Relevance of management and feeding regimens on life expectancy in captive deer

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Objective—To establish a demographic approach to facilitate the comparison of husbandry success for deer species in zoos and to test for factors that influence the performance of deer species in captivity.

Sample Population—Data collected from 45,736 zoo-kept deer that comprised 31 species.

Procedures—Data had been collected by the International Species Information System during the last 3 decades on zoo-kept deer around the world. The relative life expectancy (rLE) of a species (ie, mean life expectancy as a proportion of the maximum recorded life span for that species) was used to describe zoo populations. The rLE (values between 0 and 1) was used to reflect the husbandry success of a species.

Results—A significant positive correlation was found between the rLE of a species and the percentage of grass in the natural diet of the species, suggesting that there are more problems in the husbandry of browsing than of grazing species. The 4 species for which a studbook (ie, record of the lineage of wild animals bred in captivity) was maintained had a high rLE, potentially indicating the positive effect of intensive breeding management.

Conclusion and Clinical Relevance—The rLE facilitated the comparison of husbandry success for various species and may offer the possibility of correlating this quotient with other biological variables. Ultimately, identifying reasons for a low husbandry success in certain species may form the basis for further improvements of animal welfare in captivity. (*Am J Vet Res* 2010;71:275–280)

Zoo animal husbandry includes a constant quest for the improvement of husbandry conditions, veterinary care, reproduction, longevity, and animal welfare.[1–3] An important aspect of this challenge is the problem of evaluating these aims objectively. Although breeding success can be easily examined by analysis of birth rates and infant mortality rates,[4,5] an objective variable to examine husbandry quality is still lacking. So far, opinions on husbandry success are based mainly on personal communication among zookeepers, subjective observation, personal intuition, necropsy report analysis, and analysis of studbook data (ie, records of the lineage of wild animals bred in captivity).[6–10]

The mean life expectancy of zoo animals might be a promising value for an objective husbandry evaluation. Several reports[11–13] indicate that there are major differences in life expectancies among species of wild animals in captivity. It is assumed that these differences can be explained by certain biological characteristics (eg, body weight, social behavior, or feeding strategies). To investigate such correlations, analyses of the mean life expectancies of species of wild animals in captivity are required; to date, these are rare.[14]

Abbreviations

DOB	Date of birth
ISIS	International Species Information System
rLE	Relative life expectancy

For captive wild animals, the ISIS maintains a database of stock data for zoological institutions. This database includes data for more than 2 million animals of almost 10,000 species kept in approximately 750 zoos in 74 countries. The DOB and, where applicable, the date of death of every animal is documented, if known, which allows calculation of lifespans.

In ecological and demographic research, various variables and methods are available to describe and analyze population data. The life expectancy of an individual is defined as the mean lifetime remaining at a given age and depends on the mortality rate of the population. The life expectancy is an empirical value and can be used to compare various populations of the same species, which is often done in demographic studies. In a study by Clubb et al,[15] the life expectancy was signifi-

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cantly shorter for female adult elephants kept in zoos, compared with that of female adult elephants in wild or semiwild populations. An examination of improvements and regressions in life expectancy is possible by analyzing the development of life expectancy over time. A typical example is the observation of the continuing increase in human life expectancy during the last 2 centuries.[16] A second method is the determination of the age-related mortality rate (or survivorship) as a function of time, which is often used in ecological studies.[17,18] Various mathematical nonlinear functions are established to describe the resulting graphs of the age-related mortality rates.[19–21] However, variables of these growth functions have to be estimated.[22] Estimation of these factors, and the simplification of data by use of a model, may result in an imperfect reflection of the empirical statistics (ie, loose fit). Furthermore, populations of various species, and even the sexes of the same species, may be best represented by differing functions,[17] making comparisons among species difficult.

Longevity records of various species vary widely even in the same taxonomic groups.[23,24] A life expectancy of 15 years may be a desirable result in a species with a maximum recorded life span of 20 years, but less so in a species that could achieve a life span of 35 years. Therefore, it is essential to consider the maximum life span in comparative evaluations. Because the maximum life span of a species is not part of demographic models, a new approach is required to address problems inherent in the use of standard mathematical models. The logical step is to calculate the rLE of a population by expressing the mean life expectancy as a proportion of the maximum life span that a species could theoretically achieve.

Ruminants have been traditionally classified into feeding types (ie, browsers, grazers, and intermediate feeders) according to the botanical composition of their diet. There has been an ongoing debate as to whether these different feeding strategies are reflected in morphological and physiologic differences of the digestive system[25] and hence relevant for the practical feeding of zoo animals. Experience from wild animal husbandry indicates that several browsing species held in captivity, such as roe deer (*Capreolus capreolus*), moose (*Alces alces*), or giraffe (*Giraffa camelopardalis*) have a high nutrition-related mortality rate, whereas similar problems in grazing species are less frequently observed.[26,27] The purpose of the study reported here was to establish a demographic approach that facilitates the comparison of the husbandry success in different species by comparing their life expectancies in zoos and to test for factors that influence the performance of deer species in captivity.

Materials and Methods

Data source—The data set contained information on 45,736 deer that comprised 31 species (family Cervidae) as recorded between 1980 and 2007 by the ISIS. Information included the following for each deer: taxon, identification number, sex, DOB and date of death, origin (born in the wild or in captivity), and country of birth and death (or last known residence). Notably, the reason for death was not given in the data set.

Data processing—For the demographic approach used in this study, the exact life span of each animal was required and animals that were still alive (ie, those for which the exact life span had not been determined) were excluded. Thus, records of deer born in the wild, deer for which the DOB or date of death was only estimated to the closest year, or deer without a date of death (ie, that might still be alive or for which a date of death was not recorded) were deleted from the initial data set. Ages at death of the remaining 20,512 deer were calculated and presented in years, with days interpreted as a proportion of the full 365-day year to 2 fractional digits. Single birth cohorts were created, ensuring that all members died within the observation interval (ie, 1980 to 2007).

The number of records for some deer species became too small for further investigation; at least 45 deer/birth cohort were required for analysis. Data on the remaining 20 deer species were examined by calculating the rLE for each species as the arithmetic mean of the life spans of all deer (lx) within the species' birth cohort (with n deer) divided by the longevity recorded for this species ($a$max) as follows:

$$rLE = \frac{\sum_{1}^{n} l_x}{n \times a_{\max}}$$

The longevity records of the species were obtained from published reports.[23,24] When the maximum age recorded in the ISIS was higher than the reported ages in the literature, calculations were determined on the basis of the maximum age recorded by the ISIS. Resulting rLE values ranged from 0 to 1. Theoretically, an rLE of 0 indicated that all deer died at birth, whereas an rLE of 1 indicated that all deer reached the maximum life span.

The rLE was calculated under various conditions to exclude human influence on the population structure (eg, culling). Assuming that animals are usually culled before they achieve sexual maturity and that more males than females (as most species are kept in harem systems) are culled, the rLE of females that lived ≥ 2 years from DOB was considered most relevant and was calculated for each species in addition to the rLE for all deer (ie, males and females combined). This followed the assumption of Clubb et al,[15] which is that life expectancy of females is most relevant to population viability. In evaluation of the rLE of females that lived ≥ 2 years from DOB, the life expectancy was interpreted as total mean life span measured from birth and not as the remaining life span.

Swiss deer park data—To demonstrate the possibility of comparing the housing success of an individual facility to the overall mean rLE of a species, records for red deer (*Cervus elaphus*) and moose from a Swiss deer park from the last 43 years, which were not part of the ISIS data, were analyzed. Because reasons for death and culling measures were documented in these records, an rLE of deer and moose that were definitely not culled could be determined. This allowed testing assumptions of the typical culling regimes.

Statistical analysis—Analyses were performed on ISIS data for the 20 remaining deer species. Mean rLE for all deer and mean rLE of males or females that lived ≥ 2 years from DOB, respectively, were compared by use of a repeated-measures ANOVA and a subsequent Šidák correction post hoc test. Within species, the mean rLE for males was compared with the corresponding mean rLE for females by use of a paired *t* test. To test for biological and management factors potentially influencing life expectancy, correlations of the rLE of females that lived ≥ 2 years from DOB with body weight, preferred habitat, social behavior, percentage of grass in the natural diet (ie, percentage of grass in the diet the deer are naturally adapted to), and existence of an international studbook were analyzed. For this purpose, a stepwise procedure was performed. A Pearson correlation coefficient (*r*) was used to evaluate whether the rLE of females that lived ≥ 2 years from DOB was correlated with body weight or the percentage of grass in the species' natural diet. A *t* test was performed to evaluate the effect of social behavior, habitat, or existence of a studbook on the mean rLE of females that lived ≥ 2 years from DOB. In the next step, only factors that had a value of $P < 0.1$ were included in an ANOVA or regression analysis approach. To achieve normality, body weight was ln (ie, natural logarithm) transformed and percentage of grass was logit transformed. Values were reported as mean ± SD. All analyses were performed by use of a commercially available software program.[a] A value of $P < 0.05$ was considered significant.

Results

Evaluation by use of rLE—The rLE for 20 deer species included in the ISIS data was analyzed for the whole population, for all deer (male and females) that lived ≥ 2 years from DOB, for females that lived ≥ 2 years from DOB, and for males that lived ≥ 2 years from DOB (**Table 1**).[23,24,28–35] The rLE of red deer and moose of the Swiss deer park were within the range recorded for these species within the ISIS database (**Table 2**). The rLE (0.46) of nonculled red deer that lived ≥ 2 years from DOB in the Swiss deer park was especially close to the rLE (0.48) of red deer that lived ≥ 2 years from DOB recorded in the ISIS. Of the red deer in the Swiss deer park that were culled, most (211/239; 88%) culling events occurred before deer reached the second anniversary of their DOB; other culling events were spread evenly across age classes to correct the age structure of the population or to destroy overly aggressive males.

Data analysis—The mean rLE (0.20 ± 0.07) of all deer was significantly ($P < 0.001$) different from the mean rLE (0.41 ± 0.07) of deer that lived ≥ 2 years from DOB. Differences between the rLE of all deer and the rLE of females that lived ≥ 2 years from DOB or the rLE of males that lived ≥ 2 years from DOB, respectively, were also significant ($P < 0.001$). The mean rLE (0.25 ± 0.08) of females and the mean rLE (0.43 ± 0.07) of females that lived ≥ 2 years from DOB were significantly ($P < 0.001$) higher than the mean rLE (0.16 ± 0.07) of males and the mean rLE (0.37 ± 0.08) of males that

Table 1—The rLE of 20 deer species that lived ≥ 2 years from DOB along with data on maximum age, body weight, social behavior, habitat, percentage of grass in natural diet, and existence of an international studbook.

Species	Cohort (n)	Maximum age (y)	Body weight of females (kg)	Social behavior[30]	Habitat[30]	Grass (%)[31]	Studbook[28]	rLE2	rLE2 females	rLE2 males
Moose *(Alces alces)*	154	27.0[24]	375[29]	A	1	2	No	0.27	0.27	0.27
Mule deer *(Odocoileus hemionus)*	113	23.0*	56[29]	B	1	11	No	0.29	0.30	0.24
Reeves' muntjac *(Muntiacus reevesi)*	228	23.2†	16[29]	A	1	10[32]	No	0.33	0.36	0.29
White-tailed deer *(Odocoileus virginianus)*	257	23.0†	71[29]	B	1	3	No	0.36	0.37	0.38
Sika deer *(Cervus nippon)*	161	25.4[23]	40[29]	B	1	50	No	0.34	0.39	0.28
Sambar deer *(Cervus unicolor)*	65	26.4[23]	162[29]	B	2	50[33]	No	0.38	0.41	0.34
Fallow deer *(Dama dama)*	290	25.0[24]	97[29]	B	1	46	No	0.37	0.42	0.28
Reindeer *(Rangifer tarandus)*	319	21.8†	107[29]	B	1	36	No	0.39	0.42	0.32
Red brocket *(Mazama americana)*	112	17.1†	40[30]	A	2	1	No	0.41	0.44	0.37
Pampas deer *(Ozotoceros bezoarticus)*	56	15.0†	40[30]	A	2	80[33]	Yes	0.45	0.44	0.46
Indian muntjac *(Muntiacus muntjak)*	48	23.2*	27[29]	A	2	10	No	0.48	0.46	0.52
Southern Pudu *(Pudu puda)*	87	18.3†	9[30]	A	1	3[34]	Yes	0.46	0.46	0.46
Axis deer *(Axis axis)*	714	20.8[24]	80[29]	B	2	70	No	0.40	0.46	0.30
Chinese water deer *(Hydropotes inermis)*	436	12.7†	17[29]	A	1	50	No	0.47	0.47	0.48
Roe deer (*Capreolus capreolus*)	139	17.0[24]	52[29]	A	1	9	No	0.39	0.47	0.28
Barasingha *(Cervus duvaucelii)*	245	21.3[23]	189[30]	B	2	75[35]	Yes	0.43	0.48	0.36
Eld's deer *(Cervus eldii)*	171	21.3*	79[29]	B	2	65	Yes	0.45	0.49	0.38
Red deer *(Cervus elaphus)*	153	26.8[24]	273[29]	B	1	47	No	0.48	0.50	0.41
Père David's deer *(Elaphurus davidianus)*	159	23.3[24]	150[30]	B	1	75	Yes	0.50	0.51	0.47
Hog deer *(Axis porcinus)*	71	20.9†	35[29]	A	2	50	No	0.48	0.52	0.43
Mean ± SD	ND	ND	ND	NA	NA	ND	NA	0.41 ± 0.07	0.43 ± 0.07	0.37 ± 0.08

The rLE (values between 0 and 1, where 0 indicates that all deer died at birth and 1 indicates that all deer reached their maximum life span) reflects the husbandry success of a species; species are listed in an ascending order by rLE of females that lived ≥ 2 years from DOB.

*Estimated value according to related species, as sufficient data for this species are not available. †New longevity record data were found in the ISIS.[23,24,28–35]

1 = Temperate zone habitats. 2 = Subtropical and tropical habitats. A = Predominantly solitary behavior. B = Predominantly social behavior. NA = Not applicable. ND = Not determined. rLE2 = rLE of all deer (males and females) that lived ≥ 2 years from DOB. rLE2 females = rLE of females that lived ≥ 2 years from DOB. rLE2 males = rLE of males that lived ≥ 2 years from DOB.

Superscript numbers are reference citations for source of data.

Table 2—Comparison of rLE of red deer and moose as recorded in the ISIS and from the Swiss deer park.

	ISIS data			Swiss deer park data		
Species	Cohort (n)	rLE	rLE2	Cohort (n)	rLE_{nc}	$rLE2_{nc}$
Moose *(A alces)*	154	0.14	0.27	48	0.11	0.25
Red deer *(C elaphus)*	153	0.24	0.48	87	0.20	0.46

rLE_{nc} = rLE of deer and moose that were definitely not culled. $rLE2_{nc}$ = rLE of deer and moose that lived ≥ 2 years from DOB and were definitely not culled.
See Table 1 for remainder of key.

lived ≥ 2 years from DOB, respectively. Mean difference between rLE of females and rLE of males was 0.09 ± 0.04, and mean difference between rLE of females that lived ≥ 2 years from DOB and rLE of males that lived ≥ 2 years from DOB was 0.07 ± 0.07. Mean difference between the rLE of females that lived ≥ 2 years from DOB and the rLE of males that lived ≥ 2 years from DOB of all social species was 0.09 ± 0.05 and was higher, but not significantly ($P = 0.059$), than the mean difference for the same comparison in solitary species (0.04 ± 0.08).

Regression analysis revealed that only the percentage of grass in a species' natural diet remained a significant ($R^2 = 0.271$; $P = 0.019$) predictor of rLE of females that lived ≥ 2 years from DOB. The inclusion of a second independent variable never led to an improvement of fit. There was no correlation between rLE of females that lived ≥ 2 years from DOB and maximum body weight of females ($r = 0.104$; $P = 0.662$). Species from tropical habitats, compared with those from temperate habitats, had a higher rLE of females that lived ≥ 2 years from DOB, but this finding was not significant ($P = 0.053$). The rLE of females that lived ≥ 2 years from DOB was positively correlated ($r = 0.521$; $P = 0.019$) to the percentage of grass in the natural diet (ie, the rLE increased with a higher percentage of grass in a species' natural diet). The mean rLE of females that lived ≥ 2 years from DOB of 5 species (Table 1) for which a studbook was maintained was higher than that of species without a studbook, but this difference was not significant ($P = 0.093$).

Discussion

The rLE is used to describe the development of captive animal populations and can be defined as the mean life expectancy of a species as a proportion of the maximum recorded life span for that species. It is an empirical value that can be easily calculated for any demographic data set for the whole population or any subpopulation (eg, only females or only adult animals). The following characteristics of the rLE facilitate comparative studies among species: first, the rLE is a single value describing a given cohort in a precise manner, which is deduced from the life spans of the individual animals; second, the relation to the longevity record of a species (the interpretation of mean life expectancy as a proportion of the longevity record) eliminates problems associated with the fact that various species have different maximum life spans.

It is important to exclude human influences (eg, culling) on the population structure to examine the mean life expectancy as a variable of a species' husbandry success in captivity. It is assumed that most animals are culled before they achieve sexual maturity and that more males than females are culled.[36] In the present study, this led to the hypothesis that the rLE of females that lived ≥ 2 years from DOB is most relevant in terms of analyzing rLE of a captive species. To test this hypothesis, data on red deer and moose of a Swiss deer park with a known culling management were compared with data on the same species included in the ISIS data set. Most (88%) culling events of red deer in the Swiss deer park were completed before deer reached the second anniversary of their DOB. In the present study, the rLE values between the 2 groups of red deer that lived ≥ 2 years from DOB (rLE of 0.46 for nonculled deer in the Swiss deer park vs rLE of 0.48 for deer recorded in the ISIS) were close, supporting the fact that culling usually takes place within the first 2 years of life or before animals achieve sexual maturity.

In the study reported here, females had significantly higher rLE values than males by use of both rLE approaches (ie, use of rLE of all deer and use of rLE of deer that lived ≥ 2 years from DOB). These findings may reflect differences in culling practices for males and females or differences in mortality patterns between males and females. Polygynous deer species are usually kept in harem groups consisting of 1 male and several females, whereas primarily solitary species are mostly kept in pairs (1 male and 1 female). As a result of a smaller demand and less available space for males of polygynous species, differences in culling practices for males and females should be more evident in these species. The difference in the rLE between males and females that both lived ≥ 2 years from DOB was higher (but not significantly)for social species than for solitary species. This finding suggests that more males than females were culled. Additionally, it is a common finding in natural mammalian populations that juvenile and adult males have higher mortality rates than do females. Reasons for this phenomenon in free-ranging populations, such as expression of deleterious recessive alleles on the X chromosome, smaller parental investment in male offspring, lower resistance to food shortage as a result of higher growth rates with higher energy demand of males, sexual size dimorphism, and an intense intrasexual competition in polygynous species, are discussed in the literature.[37–41] The culling management in zoological institutions and the higher mortality rate in newborn and young nonadult males indicate that adult female

life expectancy is the most useful measure for demographic analysis of zoo populations.

The calculated rLE of captive-born animals of 20 deer species from the ISIS data set mirrors the husbandry success in zoos during the last 27 years. By ranking the rLE of various deer species, it is possible to identify those species that may have special husbandry requirements and therefore need special care. Assuming that an rLE of females that lived ≥ 2 years from DOB of > 0.41 (reached in 15/20 deer species in this report) is a comparatively good value, special efforts are required to improve the husbandry success of moose, mule deer (*Odocoileus hemionus*), Reeves' muntjac (*Muntiacus reevesi*), white-tailed deer (*Odocoileus virginianus*), and sika deer (*Cervus nippon*). Especially in the case of moose, numerous reports on the difficulties that occur in the husbandry of this species have been published, as reviewed by Clauss et al.[9]

For the deer populations reported here, only the percentage of grass in the natural diet of the species was significantly associated with the rLE of females that lived ≥ 2 years from DOB. The percentage of grass in a species' natural diet allows for classification of animals as browsers (low percentage of grass in its natural diet) or grazers (high percentage of grass in its natural diet).[25] In the step-up procedure, only the percentage of grass remained a significant predictor of rLE of females that lived ≥ 2 years from DOB, which demonstrates that species adapted to browse (small amounts of grass in its natural diet) do not perform as well in captivity. This conclusion is supported by a study by Müller et al[42] that found a shorter life expectancy of captive roe deer (a browser), compared with that of 2 free-ranging populations of these deer. By comparison, mixed-feeding reindeer (*Rangifer tarandus*) and red deer had longer life expectancies in captivity. It has been suggested that 1 typical characteristic of several browsing ruminants held in captivity is their reluctance to ingest grass hay or even lucerne hay-forages in adequate amounts,[26] which are the major components of ruminant diets in most zoos. Reasons for the general reluctance to ingest such feeds could lie in a rumen that is not equipped to handle the degree of stratification these forages induce when ingested in large quantities[43] or a dentition that is not adapted to a proper comminution of these roughages.[13,44,45] Whatever the cause, a reduced forage intake will automatically result in a higher proportion of concentrates in the ingested food, thus enhancing the danger of an ensuing acidosis. Comparative investigations on acidosis in captive ruminants are rare.[26] Nevertheless, the trend of increasing fiber content in pelleted feeds marketed for browsing wild ruminant species in captivity[27] indicates that fiber intake in these species via the usually offered roughage is not guaranteed. Findings of the study reported here should be considered as an incentive to improve current feeding practices in zoos, especially in the diets of large browsing species like moose, by offering more varied roughage sources, high-fiber compound feeds, and more browse.[27,46]

Several international studbooks are maintained for deer species (Table 1) and certain subspecies (Vietnamese sika deer [*Cervus nippon pseudaxis*]). In the study reported here, the mean rLE of females that lived ≥ 2 years from DOB for 5 deer species with a studbook was higher than that of species without a studbook, although this difference was not significant. A potentially higher husbandry success of species for which a studbook is maintained may reflect the higher attention provided to more valuable species, compared with more common hoofstock. It is also possible that adherence to explicit husbandry guidelines usually provided in studbook updates, or the avoidance of crowding conditions caused by more frequent translocation of individuals to other facilities, has a positive effect on the rLE of a species.

Most zoos that contribute data to the ISIS are located in North America or Europe within the temperate climate zone. In the study reported here, a higher rLE in deer derived from temperate climates was expected, compared with that of species that originate from subtropical and tropical habitats, as the latter ones may be more prone to infectious diseases and climate stress. The finding that deer species from subtropical and tropical climates had a higher (although not significantly higher) rLE than that of species from temperate climates was surprising and may be an effect of heated housing during winter, which is usually not offered for deer species from temperate zones.

On the basis of the findings of this study, conclusions on differences in the husbandry success between wild-caught and captive-born deer are not possible. Because the exact life span of each deer was required for the rLE approach, information on wild-caught deer (for which a DOB, and hence the exact age, was not available) had to be excluded from the analysis. Further investigations are necessary to prove the common suggestion that animals born in captivity have a higher life expectancy, compared with wild-caught animals, because of better adaptation to the zoo environment. Clubb et al[15] disproved this assumption for Asian elephants, as captive-born Asian elephants had a poorer adult survivorship than their wild-born conspecifics.

a. SPSS, version 16.0, SPSS Inc, Chicago, Ill.

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Mating system, feeding type and *ex situ* conservation effort determine life expectancy in captive ruminants

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Zoo animal husbandry aims at constantly improving husbandry, reproductive success and ultimately animal welfare. Nevertheless, analyses to determine factors influencing husbandry of different species are rare. The relative life expectancy (rLE; life expectancy (LE) as proportion of longevity) describes husbandry success of captive populations. Correlating rLE with biological characteristics of different species, reasons for variation in rLE can be detected. We analysed data of 166 901 animals representing 78 ruminant species kept in 850 facilities. The rLE of females correlated with the percentage of grass in a species' natural diet, suggesting that needs of species adapted to grass can be more easily accommodated than the needs of those adapted to browse. Males of monogamous species demonstrate higher rLE than polygamous males, which matches observed differences of sexual bias in LE in free-living populations and thus supports the ecological theory that the mating system influences LE. The third interesting finding was that rLE was higher in species managed by international studbooks when compared with species not managed in this way. Our method facilitates the identification of biological characteristics of species that are relevant for their husbandry success, and they also support ecological theory. Translating these findings into feeding recommendations, our approach can help to improve animal husbandry.

Keywords: animal husbandry; browser; artiodactyls; life expectancy; sexual bias; zoo

1. INTRODUCTION

In 2003, the international zoo community claimed '*to exercise the highest standards of animal welfare*' [1]. The importance of this aim cannot be overvalued, as ethical considerations of zoo critics conclude that keeping animals in zoos is only acceptable if their welfare is guaranteed [2,3]. Important questions arise from the call for '*highest standards of animal welfare*' in zoos: how can we measure welfare, and how can husbandry success be improved [4]? Even though an increasing number of articles have been published in this field, most articles are theoretical [5]. Behavioural patterns (occurrence of stereotypies), metabolic parameters (blood and faecal corticosteroid concentrations), health status (prevalence and incidence of diseases) and life-history data (breeding success, life expectancy (LE)) were discussed as feasible indicators of wellbeing in zoos [6,7].

In their collaborative effort to manage self-sustaining populations, the zoo community started pooling their population data in a common database, managed by the International Species Information System (ISIS). ISIS have collected individual animal data from approximately 850 member institutions in over 80 countries since 1973. Considering all single zoo populations of one species as parts of one metapopulation, ISIS data allow calculations of parameters characterizing the *average* zoo population. To estimate the development of a metapopulation, calculations of life-history parameters (e.g. annual mortality and LE) are required. For example, Clubb [8] calculated that adult female elephants (*Elephas maximus* and *Loxodonta africana)* had shorter life expectancies in zoos compared with wild and semi-wild reference populations.

Comparative analyses of different species' performance in captivity are particularly valuable to detect factors influencing husbandry success. Unfortunately, such analyses are still relatively rare. Clubb & Mason [9–11] demonstrated that frequencies of stereotypies and the extent of infant mortality in captive carnivores were higher in wide-ranging species when compared with species with smaller home range sizes. As LE of different species correlates generally with the body mass of the species (allometric principle [12]), such comparative analyses of LE require a correction for this factor. In one survey of life-history data from 20 deer species kept in captivity, the relative LE (rLE; *average* LE as proportion of *maximum* LE) of adult females correlated positively with the percentage of grass in a species' natural diet (%grass) [13]. These examples demonstrated that interspecies comparisons of behavioural measures or

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life-history data allow the detection of biological characteristics that are relevant for the adaptability of species to live under the conditions in captivity.

Here, we use such a comparative approach (rLE of metapopulations) to analyse biological factors correlated to husbandry success in 78 ruminant species. We expect that not only browsing deer, but also browsing ruminants, in general, perform less successfully in captivity compared with mixed feeders and grazers. Species from the tropics and subtropics should have more problems coping with climatic conditions in the temperate zone (where the majority of ISIS zoos are located), and thus should display a lower rLE compared with species originating from the temperate zones. Compared with wild populations, captive zoo animals are confronted with much higher population densities. Density-dependent influences on LE (social stress, contact with pathogens) should have a higher impact in solitary and pair-living species, which are less adapted to crowded conditions (as in zoos). Males that defend a harem have a higher investment in reproduction compared with monogamous species, so that males of polygamous species may have a lower LE. Additionally, we test the hypothesis that species intensively managed by an international studbook perform better than those unmanaged, assuming that husbandry of such focus species is performed with particular care.

2. MATERIAL AND METHODS

For this investigation, data from 166 901 animals, representing 78 species held in captivity (suborder Ruminantia) were analysed. The data were collected by the ISIS. Data preparation followed the same procedure as described by Müller *et al.* [13]. LE of a species' birth cohort was expressed separately for both sexes as rLE (LE of a cohort as a proportion of the record longevity of the species) to exclude allometric influences. Only animals that lived 2 years from date of birth were included, to exclude a bias owing to the culling of surplus young animals. Ranging from 0 to 1, an rLE of 0 would denote the death of all individuals at birth, whereas an rLE of 1 implies that all individuals reached the maximum lifespan.

To analyse the influence of biological and husbandry factors on the rLE, literature data on body mass, geographical origin, social behaviour (in case of females), mating system (in case of males), percentage of grass in the natural diet of a species, as well as the existence of an international studbook, were included in a step down linear regression approach as independent variables (separately for both sexes; see the electronic supplementary material for details). To achieve normality, some of the variables were log-transformed in advance. In order to avoid the false interpretation of ancestry-based correlations in these models as adaptation (i.e., finding a significant result simply because related species behave in a similar manner) [14,15], the analyses were controlled for phylogenetic influences using the 'phylogenetic generalized least-squares' method (PGLS; [16,17]; see the electronic supplementary material for details and phylogenetic tree). This procedure estimates a covariance matrix of the species owing to their ancestral roots and includes these inter-relationships in a generalized least-squares algorithm to determine the model parameters. For comparison purposes, respective generalized linear models (GLMs) without phylogenetic control were set-up. The statistical calculations were performed with SPSS 16.0 (SPSS Inc., Chicago, IL, USA) and COMPARE 4.6 programme [17]. The significance level was set to $\alpha < 0.05$.

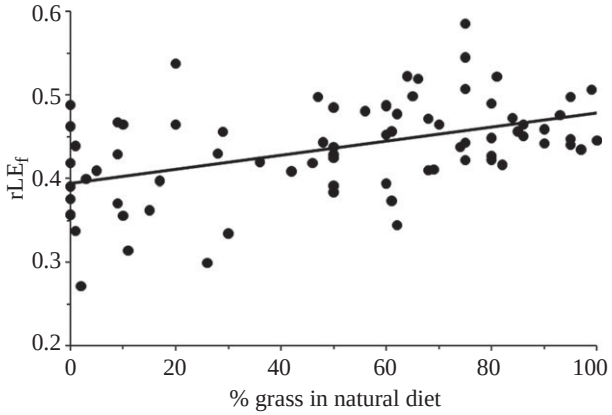

Figure 1. Positive correlation of the relative life expectancy (rLE) of females that lived 2 years from date of birth (rLE_f) with the percentage of grass in a species' natural diet (%grass). Note that species with low %grass (browsers) demonstrated lower rLE_f compared with species with medium and high %grass (intermediate feeding type and grazers). The relationship was significant (see the electronic supplementary material, table S1).

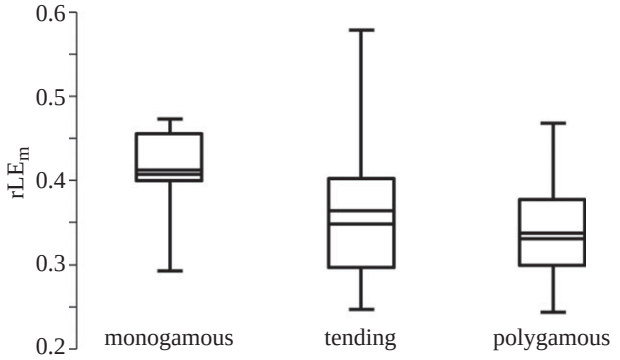

Figure 2. Range, arithmetic mean and quartiles of the rLE of males that lived 2 years from date of birth (rLE_m) according to mating type. Note that males of monogamous species had a higher rLE compared with polygamous species. The relationship was significant (see the electronic supplementary material, table S1).

3. RESULTS

Within species, an rLE of females was significantly higher than an rLE of males (paired *t*-test, $p < 0.001$, $n = 78$ species; see the electronic supplementary material for details). In females, the step-down procedure identified %grass (figure 1) and the presence of an international studbook as the only significant factors influencing rLE. In males, we identified mating type (figure 2) and also the presence of an international studbook as the only significant factors influencing rLE (table 1). The resulting models were identical for analyses with and without PGLS.

4. DISCUSSION

Our study identified biological characteristics of species that had an influence on husbandry success in the past, allowing suggestions for improvements in husbandry.

Table 1. Results of final GLMs. (Independent variables remained after a step-down procedure starting with %grass, studbook, mating system (or social system, alternatively), habitat and ln(body mass). Results given for GLMs without and with phylogenetic generalized least squares (PGLS; likelihood ratio test). Independent variables assessed: body mass, percentage of grass in the natural diet, social system or mating system (alternatively), natural habitat (temperate versus subtropical/tropical) and presence of an international studbook.)

	GLM F, p	GLM (PGLS) χ^2, p
dependent variable: rLE_{2f}		
%grass	$F_{1,75} = 19.84$, $p < 0.001$	$\chi^2 = 8.28$, d.f. = 1, $p = 0.004$
studbook	$F_{1,75} = 7.69$, $p = 0.007$	$\chi^2 = 8.80$, d.f. = 1, $p = 0.003$
dependent variable: rLE_{2m}		
mating system	$F_{2,74} = 6.719$, $p = 0.002$	$\chi^2 = 9.92$, d.f. = 2, $p = 0.007$
studbook	$F_{1,74} = 6.745$, $p = 0.011$	$\chi^2 = 5.52$, d.f. = 1, $p = 0.019$
dependent variable: rLE_{2m}		
social system	$F_{2,74} = 5.420$, $p = 0.006$	$\chi^2 = 9.76$, d.f. = 2, $p = 0.008$
studbook	$F_{1,74} = 5.177$, $p = 0.026$	$\chi^2 = 4.34$, d.f. = 1, $p = 0.037$

The data on rLE generated in this study (see the electronic supplementary material for details) can serve as global averages, against which a zoo can compare its populations, in the form of an in-house quality control and warning system.

So far, the effect of particular husbandry measures is rather assessed by approaches investigating single species than by comparative analyses between species. Different studies demonstrate that environmental enrichment, feeding management or exposure to the public influence the excretion of corticoids, indicating different stress responses [19]. Our analysis does not test for such husbandry-related factors, but identifies biological characteristics that describe the adaptability of a species to live under captive conditions. The results allow two different conclusions whether species with a low rLE should be kept: either try to optimize husbandry, or focus on species in which a higher husbandry success can more easily be achieved.

Contrary to our prediction that social behaviour of a species (measure to live under crowded conditions) influences rLE of female ruminants, such a correlation could not be detected. It is conceivable that the common practice of keeping solitary species in pairs in large enclosures prevents a negative impact on rLE. Additionally, no relationship between the geographical origin of a species and an rLE was observed, indicating that climatic stress in (sub-)tropic species that are kept in the temperate zone does either not play an important role, or that winter housing in heated stables eliminates the influence on rLE.

In adult female ruminants, the percentage of grass in a species' natural diet was positively correlated to the rLE in captivity. This parameter characterizes the diet a species is physiologically adapted to (not the one fed in zoos), and indicates whether a species is a browser (very low percentage of grass in the natural diet), mixed feeder or grazer [20]. Our results corroborate the subjective experience that browsers demonstrate a higher nutrition-related mortality in captivity and are more challenging to keep when compared with grazing species, owing to the complex logistics of providing browse [21]. In captivity, browsers are often offered grass hay and/or lucerne hay as surrogate roughage sources. The reluctance of browsers to ingest such roughage sources in larger amounts, as either their teeth or their stomachs are not adapted to the physical properties of these materials [22,23], leads to an increased proportion of concentrate feeds in the ingested diet. This will cause chronic forestomach acidosis, which in turn leads to a higher incidence of a variety of diseases [24] and ultimately to a shorter average LE.

The diet a species is naturally adapted to was not a predictor of LE in male ruminants. Instead, mating type had a significant influence on LE, with males of monogamous species demonstrating a higher LE than territorial males, or males defending a harem. Lower annual survival rates in males when compared with females are a common characteristic in population dynamics of free-living wild ungulates [25]. The here-described lower rLE of male ruminants in captivity proves that this pattern can also be observed in captive populations. This is particularly interesting, as the pressure of the rut is expected to be much lower in captivity, where usually only one adult male is kept in a harem, when compared with the situation in the wild, where several males compete for the females. In one experimental study on wild-living soay sheep (*Ovis aries*), castrated males demonstrated a prolonged LE compared with intact males and even females [26]. Both findings together support speculations that not only an intensive intraspecific competition for females during the rut, but also reproductive physiology *per se* has a negative influence on male LE. In free-living mammal populations, the degree of male-biased adult mortality correlates positively to the degree of sexual size dimorphism [27]. Sex differences in adult longevity are more pronounced in polygynous (degree of sexual dimorphism correlates with degree of polygyny [28]) when compared with monogamous species [29]. Two results of our analysis support the theory that sexual dimorphism and mating system explain the pattern of sexual bias in adult LE of ungulates: (i) rLE in captive males of ruminant species with lower male reproductive investment (monogamous species) was higher compared to species with higher investment (polygynous species), and (ii) the difference between the rLE of females and males of monogamous species was significantly smaller than the difference between female and male rLE in polygynous species. Nevertheless, an influence of culling measures on the observed sexual bias of adult LE with respect to mating systems cannot be completely excluded, although recommendations for population management of the World Association of Zoos and Aquariums [30] and the results of Müller *et al.* [13]. suggest that culling is performed before animals are sexually mature.

One major past achievement of zoos was the conservation of species that went extinct in the wild, including Przewalski's horse (*Equus caballus przewalskii*) and Père David's deer (*Elaphurus davidianus*). A major key to this

success was the breeding coordination of many zoos with international studbooks. Nowadays, endangered species' conservation by *ex situ* breeding programmes is one of the most important aims of zoological institutions [1], and over 150 international studbooks have been established. The principle aim of such studbooks is to maintain a broad genetic diversity by reducing inbreeding to a minimum. Additionally, detailed husbandry recommendations including spatial requirements, housing facilities, group composition and feeding regimes are often an integral part of these studbooks. In both, male and female ruminants, rLE was higher in species managed with the help of an international studbook. Newborn mortality of several species in captivity was higher in inbreed compared with non-inbreed individuals [31–33], suggesting that inbreeding may also have an influence on adult LE. It is possible that both, the effort to reduce inbreeding in studbook-managed populations (as compared with non-managed species), or the implementation of the detailed husbandry guidelines, resulted in the higher rLE values of the respective species. The success of such an intensive population management should encourage more widespread use of studbook coordination in additional species.

Further analyses will demonstrate whether factors like inbreeding or geographical distribution of zoo populations also influence LE in captivity, and whether analyses of other taxa identify more parameters that are relevant for the husbandry success of wild species in captivity.

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Mating system, feeding type and ex-situ conservation effort determine life expectancy in captive ruminants

Supplements

Methods

Data preparation

For this investigation, data from app. 166 901 animals, representing 78 species held in captivity (suborder Ruminantia) were analysed. The data were collected by the International Species Information System (ISIS) between 1980 and 2008 and originated from 850 member institutions around the world. Information included the taxon, a personal identification number, its sex, birth and death dates, and the country of birth and death. The causes of death as well as information on the zoos where the animals lived were not included in the dataset.

Data preparation followed the same procedure as described by Müller and others [1], excluding all animals from the analysis whose exact lifespan could not be determined. Lifespans (i.e. age at death) of the remaining animals were calculated. Depending on the longest lifespan for each species recorded in the ISIS dataset, birth cohorts were determined. The birth cohort of each species was considered as belonging to one metapopulation, representing the "typical" zoo population [2]. It was not possible to calculate life expectancies separately for each zoo keeping the species (and a subsequent calculation of the average zoo median) in order to minimise a bias of the metapopulations' life expectancy due to single institutions with high stocking numbers and a very successful or unsuccessful husbandry, as zoo-specific data were not given. As almost all species are kept in more than 10 institutions and often in comparable numbers, a strong bias due to single very successful/ unsuccessful but overrepresented institutions is not expected. To minimize a bias due to human influences on the population structure by culling young animals, lifespans of the remaining species were

only considered for animals that lived more than two years from the date of birth. Using the Kolmogorov-Smirnov-Test, the data distribution of each metapopulation was analysed for both sexes separately (156 tests in total). As the null hypothesis (expected normal distribution) was only rejected in 13 cases (4 female and 9 male subsets; predominantly medium sized gazelles and goats), the arithmetic mean of all lifespans was considered as reasonable parameter to describe the life expectancy of a metapopulation, again separately for males and females.

An effect of body mass on the potential lifespan of a species was excluded by using the relative life expectancy (rLE) of a species. In this rLE approach the *mean* life expectancy of a species was expressed as a proportion of a species' *maximum* reported lifespan. Ranging from 0 to 1, an rLE of 0 would denote the death of all individuals at birth, whereas an rLE of 1 implies that all individuals reached the maximum lifespan. The maximum lifespan of a species was taken from the literature. To control for the quality of used longevity records, an additional analysis was performed. The rLE values for females were re-calculated using the mean of the five longest lifespans within one cohort as maximum ($rLE_{f\ Top5}$). This resulted in a systemic increase of rLE values, as the resulting 'mean maximum lifespan' for calculation of rLE is somewhat smaller than the maximum reported lifespan of one species. Plotting $rLE_{f\ Top5}$ against the true rLE_f values, only three outliers were detected and subsequently excluded from this second analysis. These species are known to be problematic in captivity (moose, mule deer, saiga antelope), and longevity records are based on animals from the wild. In the case of mule deer, one ISIS individual reached the age of the maximum longevity in the wild, which indicates that it is reasonable to use maximum longevities reported in the literature. The correlation between $rLE_{f\ Top5}$ and the true rLE_f was analysed using a linear model. The slope of the regression line was close to 1 (0.94; r^2=0.567; P<0.001; F=95.44), which is the suspected slope if there is only a systematic increase due to a calculation with a smaller longevity maximum. Additionally, the 95% confidences interval (CI) included 1 (lower CI

limit =0.75; upper CI limit =1.13). Thus, the slope of the regression is statistically not different from 1 (Supplemental material Figure 1), supporting the quality of the longevity records used in our main analysis.

As the okapi *(Okapia johnstoni)* and the giraffe *(Giraffa camelopardalis)* can reach lifespans of more than 30 years [3], a different dataset or a different method was used to calculate their life expectancies, respectively. An international studbook is available for the okapi that includes data of all animals ever kept in zoos and was used here to calculate okapi life expectancy as per the calculations for ISIS data. To gain the required numbers of animals that died within the observation period, the birth cohort was set between 1965 and 1975. Life expectancy for giraffe was estimated. For this purpose, the apparent life expectancies of subsequent birth cohorts (i.e. 1980-1981; 1980-1982; 1980-1983 etc.) were calculated and plotted against the difference between the duration of the observation period (in case of the giraffe 27 years) and the duration of the respective birth cohort (1 to 27 years). The resulting s-shaped graph was fitted to a sigmoid function using the program TableCurve 2D*, where $f_{(x)}$ can be interpreted as life expectancy at a given maximum recorded lifespan *(x)*. The function was used to calculate the life expectancy at x=37 years – the longevity record of the giraffe as reported by Carey and Judge [3] rounded up to the next full year.

Data analysis

To analyse the influence of biological and husbandry factors on the life expectancy of a species in captivity, information on body mass, geographical origin, social behaviour (in case of females), mating system (in case of males), percentage of grass in the natural diet of a species, as well as the existence of an international studbook WAZA-studbook were collated (supplemental material Table 1). Analyses were performed for both sexes, controlling for phylogenetic influences using the “Phylogenetic Generalized Least-Squares” method [PGLS; 4,5] and, alternatively, using the raw data. We tested for interrelationships between the

variables by either determining the Pearson's correlation coefficient, or performing an ANOVA, t-test, or Chi-square test (supplemental material Table 2). The social behaviour types were classified as solitary, facultative gregarious, and gregarious; mating types as: monogamous, 'tending' (polygamous but no harems and males do not follow more than 2 females at one time), and polygamous defending a territory or a harem. The first parameter relates to the ability to live in more crowded environments, whereas the second parameter describes the reproductive investment of males. As both parameters are significantly correlated with each other (Pearson's Chi-Square Test of association; $p<0.0001$) and, additionally, describe related circumstances, they should not be included in a single model. Thus we decided to consider "social behaviour" in the analysis of female life expectancies, and "mating type" in case of the males, but repeated the analysis in both sexes with the other parameter, respectively (both models in both sexes yielded similar results, see paper table 1). Although body mass was related to other characteristics (see supplemental material Table 2: higher in grazing species, lower in monogamous species, higher in studbook-managed species), body mass itself was not correlated to rLE.

Statistical procedure

Relationships among species were inferred from a phylogenetic tree based on the complete mitochondrial cytochrome *b* gene. Respective DNA sequences were available from GenBank (http://www.ncbi.nlm.nih.gov) for all ruminant species investigated. Sequences were aligned using CLUSTALX [6], visually controlled and trimmed to identical lengths (1140 bp). To select the best-fitting nucleotide substitution model for the data, a combination of the software packages PAUP* [v.4.b10`; 7] and MODELTEST [v.3.7`; 8] was used. Analysis was based on a hierarchical likelihood ratio test approach implemented in MODELTEST. The model selected was the general time-reversible (GTR) model [9,10] with an allowance both for invariant sites (*I*) and a gamma (*G*) distribution shape parameter (α) for among-site rate variation

(GTR+*I*+*G*) [11]. The nucleotide substitution rate matrix for the GTR+*I*+*G* model was likewise calculated using MODELTEST. Parameter values for the model selected were: -lnL = 21660.1797, $I = 0.4340$, and $\alpha = 0.8426$ (8 gamma rate categories). The phylogenetic reconstruction based on these parameters was then performed using the maximum likelihood (ML) method implemented in TREEPUZZLE [v.5.2`; 12]. Support for nodes was assessed by a reliability percentage after 50.000 quartet puzzling steps; only nodes with more than 50% support were retained. The resulting tree is displayed in the supplemental material (Figure 2). The basal polytomy for familial relationships (Tragulidae, Giraffidae, Cervidae, Antilocapridae, and Bovidae) was resolved assuming it to be a soft polytomy [13]. In order to meet the input requirements for the phylogenetic analysis implemented in the COMPARE 4.6 program [14], we resolved the remaining polytomies to full tree dichotomy by introducing extreme short branch lengths ($l = 0.00001$) at multifurcating nodes. Taxa grouping in the bifurcating process followed the phylogenies proposed by Pitra et al. [15] for Cervidae and by Fernandez and Vrba [16] for all other taxa.

To achieve normality, data on body mass, female mean life expectancy, male mean life expectancy, and male relative life expectancy were ln-transformed. Statistical analyses were performed with and without accounting for phylogeny, to test for the validity of a general, functional hypothesis, and to then discriminate between convergent effects and similarity of effects due to common descent.

In order to test whether rLE is related to body mass and the biological characteristics listed above, we performed a step-down GLM procedure, separately for both sexes and starting with body mass, origin, social behaviour (females), mating system (males), percentage of grass in the natural diet, and studbook control as independent variables. In each step, the variable with the highest non-significant p-value was eliminated until equation contained only significant variables. We always had unbalanced data with no empty cells. Thus, we followed the recommendations in the SPSS manuals for data like these and used

Type III SSQ's in the non-phylogenetic calculations. In the phylogenetically controlled calculations, the COMPARE program used log-likelihood procedures and not the Minimum Least Squares approach.

The phylogenetic control was achieved using the Phylogenetic Generalized Least-Squares approach [PGLS; 4,5] in which a well-developed standard statistical method was extended to enable the inclusion of interdependencies among species due to the evolutionary process. This analysis was performed for both a set of phylogenetic trees involving branch lengths (tree 1) and their respective counterparts with equal branch lengths (tree 2), to test the robustness of the results. As there were no relevant differences in the results, only the tests using tree 1 are given. The statistical calculations were performed with SPSS 16.0 (SPSS Inc., Chicago, IL) and COMPARE 4.6 program [14]. The significance level was set to $p<0.05$.

Supplemental Results

The difference in rLE between females and males was significantly influenced by the mating system (GLM: $p<0.001$; PGLS: $p=0.003$). This difference was significantly lower in monogamous species (where it was virtually absent at 0.00 ± 0.04, n=10 species) than in 'tending' (0.07 ± 0.09, n=32 species), and polygamous species (0.11 ± 0.05, n=36 species) (Sidak post hoc tests; monogamous vs. 'tending' $p=0.012$; monogamous vs. polygamous: $p<0.001$), but not between 'tending' and polygamous species ($p=0.165$).

Data

Table 1. The relative life expectancy (rLE) of 78 ruminant species

rLE of animals that lived ≥ 2 years from date of birth for females and males along with data on longevity, body mass, percentage of grass in the natural diet, social behavior, mating type, habitat, the existence of an international studbook, and the home range size.

Species	longevity (y)	relative life expectancy		Body mass (kg)		Biological characteristics					No. animals	
		females	males	females	males	% grass	social[y]	mating type[z]	habitat[g]	studbook[aa]	females	males
Tragulus javanicus	14.1[a]	0.42	0.47	3.9[b]	3.9[f]	0[k]	1	1[g]	2	n	90	101
Tragulus napu	16.0[b]	0.49	0.47	5.9[b]	8[g]	0[j]	1	1[g]	2	n	61	44
Giraffa camelopardalis	36.3[c]	0.36	0.43	1130[f]	1400[f]	0[k]	2	2	2	n	107	112
Okapia johnstoni	33.5[a]	0.38	0.58	287.5[b]	287.5[b]	0[k]	1	2[g]	2	y	35	33
Hydropotes inermis	13.9[b]	0.42	0.44	17.4[f]	18.5[f]	50[k]	1	1	1	n	203	190
Capreolus capreolus	17.0[c]	0.47	0.28	27.6[f]	50[g]	9[k]	1	3	1	n	73	62
Odocoileus virginianus	23.0[c]	0.37	0.38	71[f]	205[g]	9[k]	2	2	1	n	125	99
Odocoileus hemionus	22.0[b]	0.31	0.25	55.8[b]	215[g]	11[k]	2	2	1	n	61	44
Mazama americana	17.1[a]	0.44	0.37	46[f]	46[f]	1[k]	1	2	2	n	61	51
Pudu puda	21.0[b]	0.40	0.40	8.3[b]	10[g]	3[l]	1	1[y]	1	y	46	39
Rangifer tarandus	21.8[a]	0.42	0.32	113.2[b]	315[b]	36[k]	3	3	1	n	175	132
Alces alces	27.0[c]	0.27	0.27	375[f]	800[g]	2[k]	2	2	1	n	77	62
Muntiacus reevesi	23.2[a]	0.36	0.29	15.8[f]	18.3[f]	10[j]	1	1[g]	1	n	116	87
Axis axis	20.8[c]	0.46	0.30	80[f]	113[f]	70[k]	2	2	2	n	333	356
Rucervus duvaucelii	23.0[b]	0.44	0.34	143[b]	283[g]	75[m]	2	3[g]	2	y	119	38
Cervus elaphus	27.0[b]	0.50	0.40	273[f]	455[f]	47[k]	2	3	1	n	91	121
Cervus eldii	20.9[a]	0.50	0.39	79[f]	150[f]	65[k]	2	3[g]	2	y	89	59
Cervus nippon	25.4[d]	0.39	0.28	96.5[b]	110[g]	50[k]	2	3	1	n	89	67
Dama dama	25.0[c]	0.42	0.28	97[f]	200[g]	46[k]	2	3	1	n	174	110
Elaphurus davidianus	23.3[c]	0.51	0.47	149[b]	200[g]	75[k]	2	3	1	y	93	61
Antilocapra americana	17.5[d]	0.36	0.33	48[f]	63[f]	15[k]	3	3	1	n	222	189
Cephalophus dorsalis	17.1[d]	0.39	0.38	24.2[h]	25[f]	0[n]	1	1[h]	2	n	47	40
Cephalophus maxwellii	14.9[a]	0.34	0.40	8[h]	12[h]	1[n]	1[h]	1[h]	2	n	56	69
Tetracerus quadricornis	17.5[a]	0.43	0.42	19[b]	22.7[f]	9[o]	1	1[g]	2	n	45	21
Boselaphus tragocamelus	21.7[c]	0.46	0.32	169[b]	270[f]	29[o]	3[g]	3	2	n	254	225
Tragelaphus angasii	20.2[a]	0.46	0.28	100.7[b]	127[f]	20[k]	2	2	2	n	241	169
Tragelaphus spekii	23.6[a]	0.41	0.27	87.5[b]	113[f]	68[k]	2	2	2	n	166	139
Tragelaphus strepsiceros	23.0[c]	0.41	0.28	210[f]	258[f]	5[k]	2	2	2	n	307	227
Tragelaphus imberbis	19.8[a]	0.46	0.38	64.5[b]	142[f]	10[k]	2	2	2	n	109	113
Tragelaphus eurycerus	22.4[a]	0.54	0.41	253[f]	405[f]	20[p]	2	2	2	y	97	60
Taurotragus oryx	23.6[c]	0.44	0.33	432.5[b]	600[f]	50[n]	3	2	2	n	218	196
Bos javanicus	26.6[b]	0.43	0.40	666.7[b]	900[g]	80[k]	3[g]	2[g]	2	y	43	35
Bos gaurus	26.2[c]	0.52	0.29	800[b]	1000[f]	66[q]	3[g]	2	2	y	58	59
Bos grunniens	25.0[c]	0.46	0.44	333[b]	1000[g]	86[r]	3	2[g]	1	n	61	48
Syncerus caffer	29.5[c]	0.44	0.28	504.7[b]	800[g]	90[k]	3	2	2	n	66	80
Bison bison	33.0[c]	0.47	0.46	497.7[b]	1000[f]	84[k]	3[g]	2	1	n	76	48
Bison bonasus	27.0[c]	0.47	0.38	500[b]	1000[b]	68[k]	2	2[g]	1	y	81	82
Alcelaphus buselaphus	20.0[c]	0.43	0.43	150[b]	225[g]	97[k]	3	3	2	n	68	59
Damaliscus pygargus	21.7[b]	0.45	0.35	84.5[b]	100[g]	100[k]	3	3[g]	1	n	135	102
Connochaetes gnou	20.9[a]	0.52	0.33	132.3[b]	180[f]	81[n]	3	3[g]	1	n	69	59
Connochaetes taurinus	21.8[a]	0.46	0.35	177[f]	270[g]	90[k]	3	3	2	n	81	95

Hippotragus equinus	18.0[a]	0.46	0.39	259[f]	300[g]	85[n]	2	3	2	n	133	99
Hippotragus niger	22.7[a]	0.48	0.38	240[g]	300[g]	93[k]	2	3	2	n	154	109
Oryx dammah	21.8[a]	0.54	0.38	177.5[b]	200[f]	75[n]	3	3[g]	2	y	221	195
Oryx gazella	24.4[a]	0.42	0.33	227[f]	240[f]	82[k]	3	3	2	n	103	104
Oryx leucoryx	23.8[a]	0.59	0.41	121.4[b]	121.4[b]	75[n]	3	3[g]	2	y	49	45
Addax nasomaculatus	25.7[b]	0.45	0.33	182.4[b]	182.4[b]	80[n]	3	3[g]	2	y	206	152
Kobus ellipsiprymnus	24.3[a]	0.49	0.32	175.3[b]	250[g]	80[k]	2	3	2	n	75	48
Kobus kob	21.9[b]	0.50	0.34	58.6[b]	120[g]	95[k]	2	3	2	n	35	41
Kobus leche	22.3[a]	0.45	0.31	96.9[f]	130[f]	95[n]	2	3	2	y	86	64
Kobus megaceros	23.7[a]	0.44	0.35	58.6[e]	120[e]	95[n]	2[e]	3[g]	2	n	51	41
Redunca fulvorufula	14.1[a]	0.51	0.44	33.8[f]	35.5[f]	99[k]	2	2	1	n	43	27
Aepyceros melampus	19.7[a]	0.49	0.35	90[g]	68.6[f]	60[k]	3	3	2	n	257	170
Neotragus moschatus	13.5[b]	0.46	0.46	7.2[b]	7.2[b]	0[k]	1[e]	1[e]	2	n	110	107
Madoqua kirkii	17.3[a]	0.40	0.40	5.5[f]	5.5[f]	17[n]	1	1	2	n	80	90
Gazella thomsonii	21.0[a]	0.45	0.29	17.6[f]	27[f]	86[p]	3	3	2	n	262	274
Gazella gazella	18.3[b]	0.34	0.24	20.8[b]	23.4[f]	62[s]	3	3	2	n	292	284
Gazella subgutturosa	16.0[a]	0.38	0.30	25.5[b]	33[f]	50[j]	3	3	1	n	798	777
Nanger dama	19.3[a]	0.44	0.32	73[b]	73[f]	48[n]	3	3	2	n	374	274
Nanger granti	16.2[a]	0.43	0.30	47.6[b]	81.8[f]	50[k]	3	3	2	n	207	170
Litocranius walleri	17.3[a]	0.36	0.41	41.3[b]	52[g]	0[k]	2	3	2	n	87	100
Antidorcas marsupialis	20.0[c]	0.33	0.29	61.4[f]	68.6[f]	30[k]	3	3	2	n	283	281
Antilope cervicapra	21.6[a]	0.37	0.27	37.5[b]	45[g]	61[o]	3	3	2	n	502	508
Saiga tatarica	15.0[e]	0.30	0.26	40.9[f]	51[f]	26[t]	3	3	1	n	133	110
Ovibos moschatus	24.0[c]	0.48	0.40	300[l]	650[l]	62[u]	3	3	1	y	74	60
Ammotragus lervia	22.0[a]	0.41	0.37	55.5[b]	140[g]	42[v]	3	2	2	n	248	215
Capra aegagrus	20.8[d]	0.43	0.38	60[b]	90[f]	28[e]	3	2	2	n	123	106
Capra caucasica	18.6[a]	0.42	0.39	60[f]	60[f]	80[w]	3	2	1	n	100	74
Capra falconeri	19.1[a]	0.39	0.43	41[b]	110[f]	60[e]	3	2	1	n	197	166
Capra ibex	20.4[a]	0.45	0.51	71.5[b]	100[f]	60[p]	3	2	1	n	105	59
Capra nubiana	19.3[a]	0.49	0.42	71.5[e]	100[e]	60[e]	3	2	2	n	108	92
Capra sibirica	22.3[d]	0.48	0.25	71.5[e]	100[f]	50[e]	3	2	1	n	73	103
Hemitragus hylocrius	18.0[e]	0.52	0.31	35.2[e]	35.2[e]	64[x]	3	2	1	n	53	68
Hemitragus jemlahicus	21.8[c]	0.42	0.32	35.2[b]	35.2[b]	75[k]	3	2	1	n	144	124
Ovis dalli	19.0[a]	0.48	0.33	57.7[b]	61.7[f]	56[p]	3	2	1	n	142	159
Ovis orientalis	23.2[a]	0.41	0.29	100[f]	230[g]	69[k]	3	2	1	n	123	150
Oreamnos americanus	19.2[b]	0.46	0.43	82.4[b]	136[f]	61[u]	3	2	1	n	98	84
Rupicapra rupicapra	22.0[c]	0.44	0.29	42[f]	62[g]	74[k]	3	3	1	n	67	37

* Source:
a) new longevity record was found in ISIS/ studbook data; b)[17]; c)[3]; d)[18]: e) estimated from close relative of comparable body mass as sufficient data were not available; f)[19]; g)[20]; h)[21]; i)[22]; j)[23]; k)[24]; l)[25]; m)[26]; n)[27]; o)[28]; p)[29]; q)[30]; r)[31]; s)[32]; t)[33]; u)[34]; v)[35]; w)[36]; x)[37]; y)[38]; z)[39]; aa)[40]
Social: 1 = solitary, 2 = facultative gregarious, 3 = gregarious; Mating type: 1 = monogamous, 2 = males follow more than one female but no harem or territory is defended, 3 = harem or territory is defended; Habitat: 1 = temperate zone, 2 = subtropical and tropical habitats

Table 2. Interrelationships between the variables (significant results set in **bold**)
Body mass, percentage of grass in the natural diet (%grass), mating type (Mating) social behaviour (Social), habitat, and the existence of an international studbook.

	Body mass (males)	%grass	Mating	Social	Habitat	Studbook
Body mass (females)	-	**r=0.396 n=78 p<0.001[a]**	**F=30.965 df=(2,75) p<0.001[b]**	**F=23.055 df=(2,75) p<0.001[b]**	t=-0.441 df=76 p=0.661	**t=-3.180 df=76 p=0.002[c]**
%grass	**r=0.357 n=78 p=0.001[a]**	-	**F=15.269 df=(2,75) p<0.001[d]**	**F=22.696 df=(2,75) p<0.001[d]**	t=0.460 df=73.9 p=0.647	t=-1.252 df=76 p=0.214
Mating	**F=36.275 df=(2,75) p<0.001[b]**	-	-	**χ^2 = 57.564 df=4 p<0.001**	χ^2 = 1.927 df=2 p=0.382	χ^2 = 0.993 df=2 p=0.609
Social	**F=26.776 df=(2,75) p<0.001[b]**	-	-	-	χ^2 = 1.519 df=2 p=0.468	χ^2 = 0.916 df=2 p=0.633
Habitat	t=-0.290 df=76 p=0.773	-	-	-	-	χ^2 = 1,094 df=1 p=0.296
Studbook	**t=-2.625 df=76 p=0.010[c]**	-	-	-	-	-

r Pearson's correlation, F ANOVA, t t-test, χ^2 Chi-square test, n sample size, df degrees of freedom

[a] Larger species consume higher percentages of grass [41 for contradictory results on this question depending on the dataset]

[b] Species with 1-2 females per males/living single or in pairs have a lower mean body mass than species of the other categories [42]

[c] Species managed via studbook have a higher mean body mass than other species

[d] Species with 1-2 females per males/living single or in pairs have a lower mean %grass than species of the other categories [42]

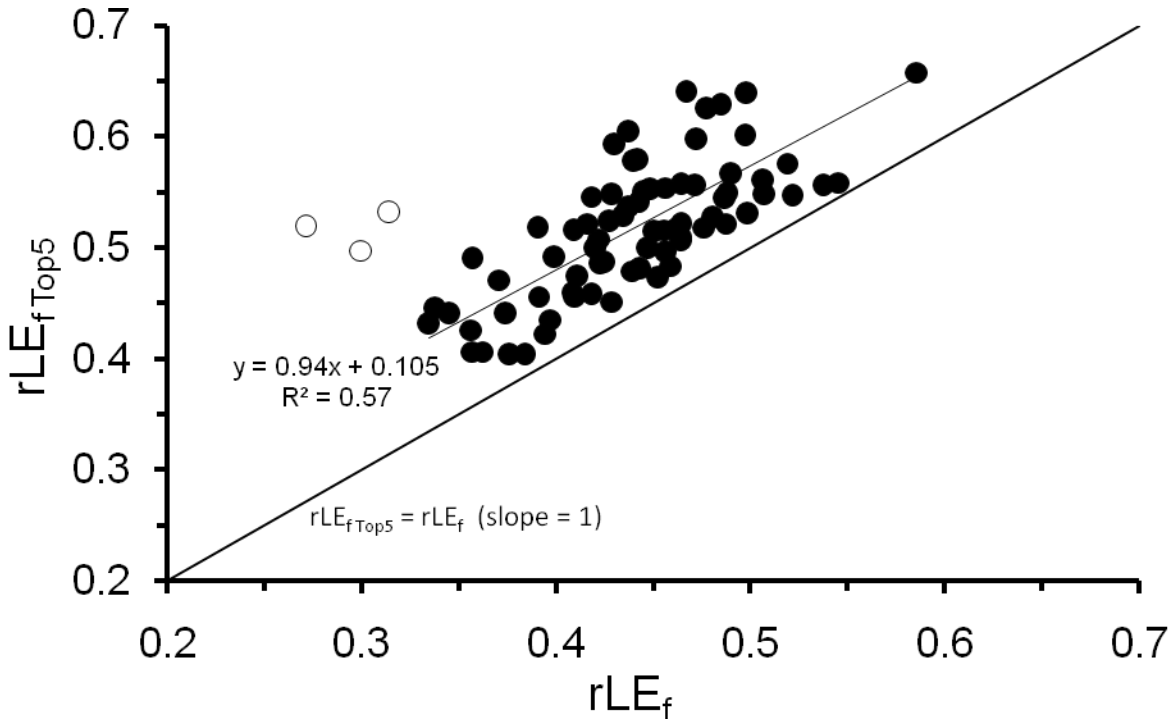

Figure 1. The relative life expectancy calculated on the basis of the five longest lifespans within an ISIS cohort (rLE_{fTop5}) is plotted against the true rLE_f values to control for quality of literature data on maximum lifespans. As the slope of the regression is not different from 1 ($p<0.001$), quality of literature data is strongly supported. Note that due to the calculation of rLE with a smaller 'mean maximum longevity' in case of $rLE_{f\,Top5}$, $rLE_{f\,Top5}$ is systematically higher (+0.105) than rLE_f.

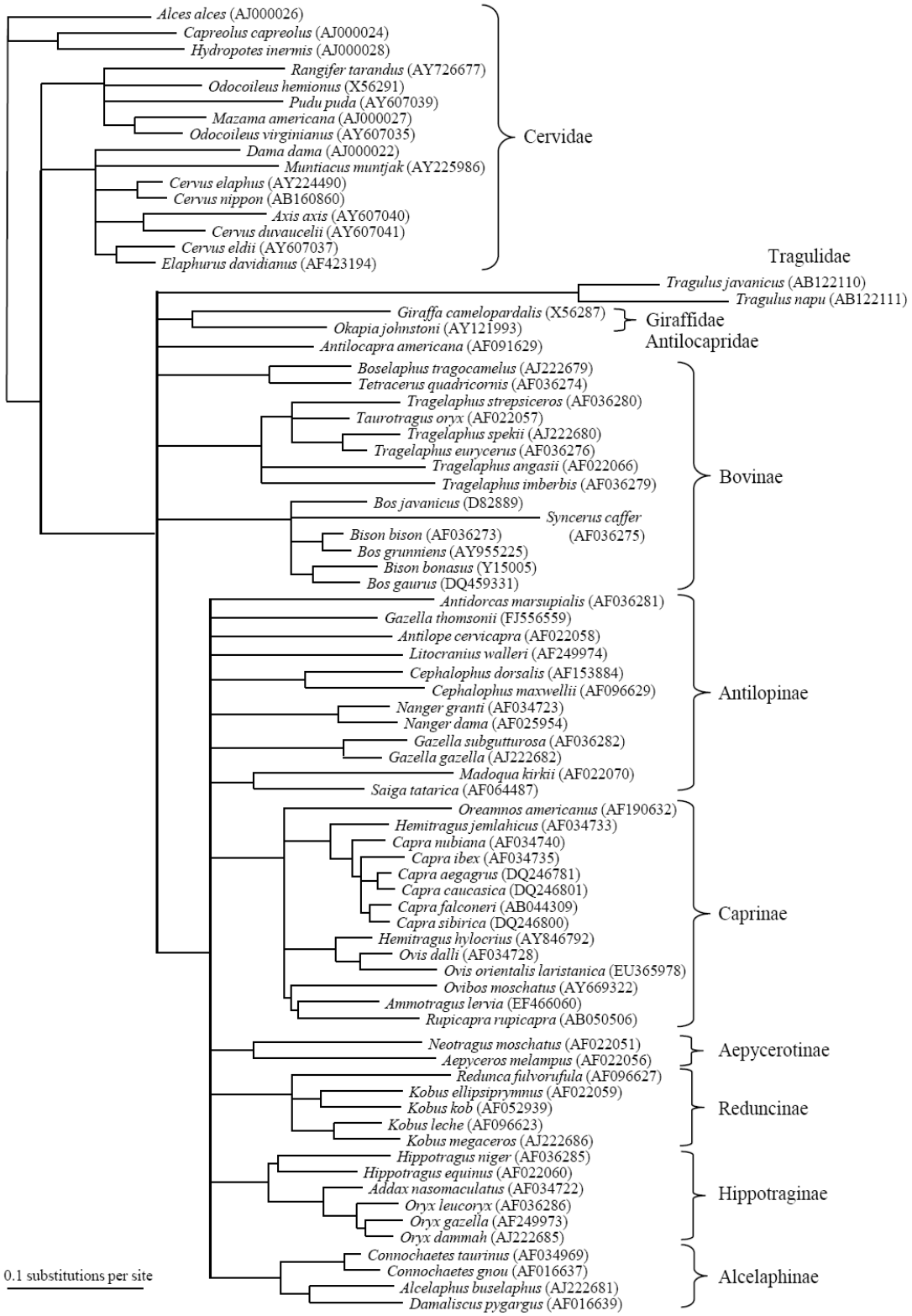

Figure 2. Fifty percent majority rule maximum likelihood tree (50,000 quartet puzzling steps), depicting the phylogenetic relationships among complete mitochondrial cytochrome b sequences from 78-ruminant taxa as used in the phylogenetically controlled statistics in this study (accession codes from GenBank available at: http://www.ncbi.nlm.nih.gov).

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